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A comparative cytogenetic study on the mitotic and meiotic chromosomes in hamster species of the genus *Phodopus* (Rodentia, Cricetinae)

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Abstract

The mitotic and meiotic chromosomes of the two hamster species *Phodopus sungorus* and *P. roborovskii* were examined with the aid of various banding techniques. *P. sungorus* has a diploid chromosome number 2n = 28. *P. roborovskii* is 2n = 34. Almost complete homoeologies can be demonstrated for all euchromatic segments. The differences in the karyotypes of the two species can be traced to eight centric fusions, three pericentric inversions, one telomeric fusion, as well as to changes in the content and arrangement of the constitutive heterochromatin. With a high degree of probability, the karyotypes of both species have developed from a common ancestor with 2n = 40 chromosomes. Both species have remarkably large, heteromorphic sex chromosomes. In male meiosis, the euchromatic arm of the X chromosome not paired with the Y chromosome exhibits highly delayed condensation throughout prophase.

Introduction

The genus *Phodopus* (Rodentia, Cricetinae) comprises two species of Asiatic hamsters. The habitat of *P. sungorus* extends from Ischim (Ural) to the west throughout the steppes of western Sibiria up into the regions of Mongolia, Djungaria and Altai to the southeast. *P. roborovskii* inhabits the northern and northeastern part of the Gobi desert, as well as the provinces Shansi, Nan-Shang and Zaidan (Argyropulo 1933).

The karyotype of the Djungarian hamster *(P. sungorus)* is well characterized with various banding techniques (Thust 1974; Pogosianz 1975; Bigger and Savage 1976; Das and Savage 1978; Gamperl et al. 1978). *P. sungorus* is being successfully used for studies on cancer, mutagenesis and chromosomal nondisjunction (Pogosianz 1975; Hansmann 1984). The reasons for the prominence of the Djungarian hamster in so many areas of research are that these animals are hardy and easy to keep and that they reproduce rapidly with quickly developing offspring. In contrast to this, no detailed cytogenetic analyses have been made with *P. roborovskii*.

The present study demonstrates the homoeologies found between the chromosomal banding patterns of *P. sungorus* and *P. roborovskii*, and the most probable common

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ancestral karyotype of these two species is proposed. The possible mechanisms involved in the chromosome phylogeny of *P. sungorus* and *P. roborovskii* are discussed.

Material and methods

Two adult male and female specimens each of *P. sungorus sungorus* and *P. roborovskii* were used for this study. Mitotic chromosome preparations were obtained from fibroblast cultures initiated from biopsies of lung and peritoneum according to the usual techniques (Wolf 1974). Male meiotic chromosomes were prepared according to the method of Meredith (1969).

For conventional karyotyping the preparations were stained with Giemsa dye (5min in a 5 % Giemsa solution, pH 6.9) after preidentifying the chromosomes by Q-banding (Caspersson et al. 1970). Chromosomal R-banding patterns were obtained using the technique of Sehested (1974). The chromosomes were numbered in accordance with the G-banded standard karyotype of *P. sungorus* established by Pogosianz (1975). Staining of the constitutive heterochromatin (C-banding) was done according to the method of Sumner (1972), and silver (Ag) staining of the nucleolus organizer regions (NORs) according to the method of Goodpasture and Bloom (1975). Preidentification of the chromosomes with quinacrine mustard (Q-banding) was necessary because not all chromosomes could be identified with certainty in Giemsa-stained, C-banded or silver-stained preparations. The fluorescence microscopy was performed using a Zeiss fluorescence microscope equipped with an 50W/AC lamp and a filter combination 450–490/FT 510/LP 520.

Length measurements of the chromosomes were made on photographs of metaphases. The film negatives were projected at a final magnification of 30,000× and the chromosome lengths were determined with a map measurer. The calculation of the nondisjunction (ND) frequency was made exactly as described by Long (1978).

Results

Both conventional staining with Giemsa dye as well as fluorescent banding patterns with quinacrine mustard of *P. sungorus* and *P. roborovskii* are demonstrated in figure 1. The karyotype of *P. sungorus* (Fig. 1a, 1c) is composed of 2n = 28 chromosomes with a fundamental number (FN) of 51 chromosome arms. With the exception of the acrocentric chromosomes 12, 13 and Y, all chromosomes are submetacentric to metacentric. No secondary constriction could be detected in any chromosome. *P. roborovskii* (Fig. 1b, 1d) has a diploid chromosome number of 2n = 34, the fundamental number is 59. Autosome pairs 12, 14 to 16 as well as the Y chromosome are acrocentric, all others are submetacentric to metacentric. Chromosomes 12 and 14 possess secondary constrictions located close to the centromeres. After staining with the AT-specific fluorescent dye quinacrine mustard (Fig. 1c, 1d), the chromosomes exhibit distinct banding patterns (Q-bands) enabling the unequivocal identification of all chromosomes of the two hamster species. No brilliant quinacrine fluorescence characteristic for AT-rich heterochromatic regions could be demonstrated.

The C-banded karyotypes of *P. roborovskii* and *P. sungorus*, preidentified by their Q-bands, are depicted in figure 2a and 2b respectively. In both species, constitutive heterochromatin is localized in the centromeric regions of most autosomes. The autosomes 1, 2 and 4 of *P. roborovskii* and the autosomes 1, 5 and 12 of *P. sungorus* are characterized by unusually sparse centromeric C-bands. Interstitial C-bands are evident in the autosomes 3, 5 and 7 of *P. roborovskii* and in the autosomes 1, 2, 4, 6 and 7 of *P. sungorus*. As the comparison of R-banding patterns (Fig. 4) shows, the interstitial heterochromatic segments in the autosomes 3 and 7 of *P. roborovskii* are homoeologous to the interstitial C-bands in the autosomes 2 and 6 of *P. sungorus*. The Y chromosome and one arm of the X chromosome are completely heterochromatic in both species. Large amounts of constitutive heterochromatin are localized in the pericentromeric regions of autosomes 11 and 13, as well as to both sides of the secondary constrictions in autosomes 12 and 14 of *P. roborovskii* (Fig. 2a). The X chromosome of *P. sungorus* comprises 9.9 % of the haploid female karyotype, whereas in *P. roborovskii* it is only 6.7 %.

The nucleolus organizer regions (NORs) of the two hamster species can be specifically demonstrated by using the ammoniacal silver staining (Fig. 3). All metaphases were prestained with quinacrine mustard to identify the NOR-carrying chromosomes. In *P. roborovskii,* the NORs are concentrated in the long arms of chromosomes 12 and 14 (Fig. 3a), which exhibit distinct secondary constrictions in conventionally stained preparations

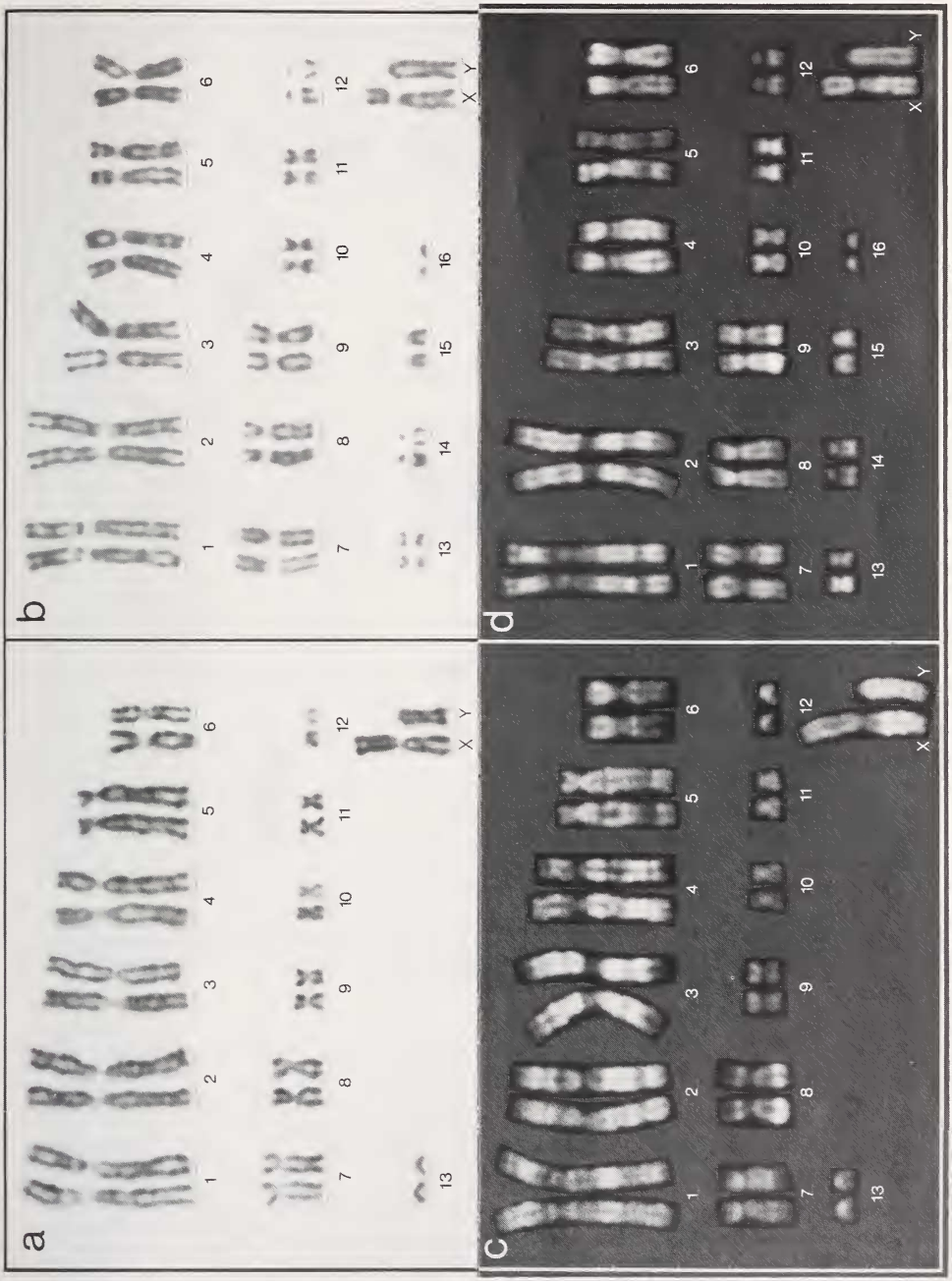

Fig. 1. Karyotypes of male *P. sungorus (left)* and *P. roborovskii (right).* (a, b) Conventional staining with Giemsa dye. (c, d) Fluorescent banding patterns obtained after staining with quinacrine mustard

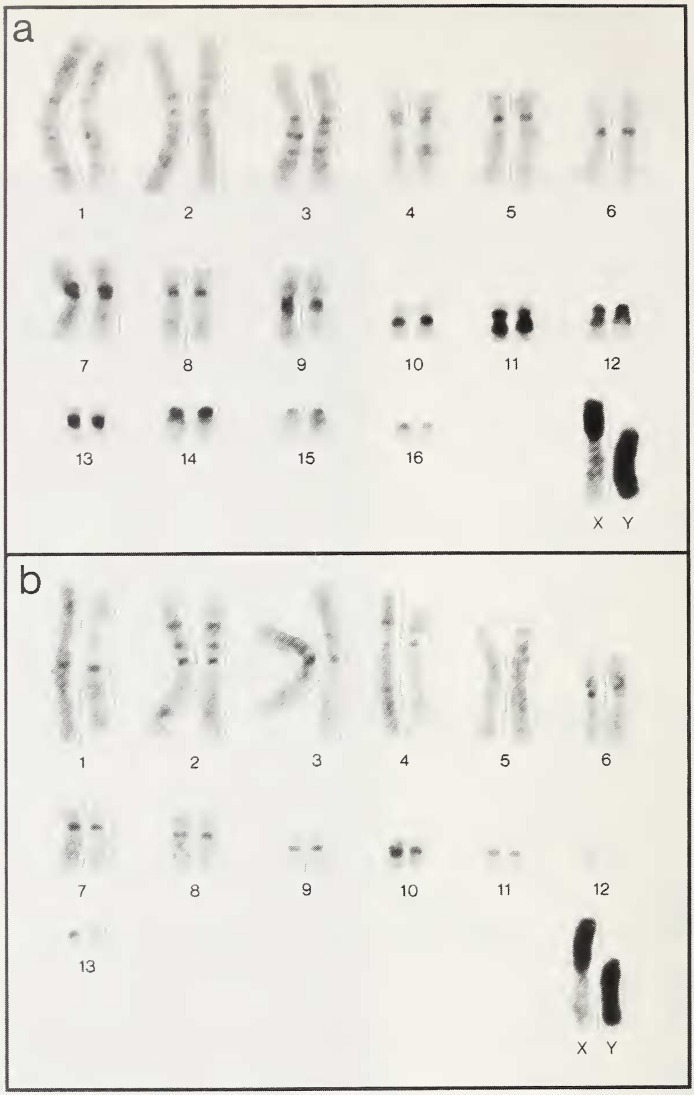

Fig. 2. C-banded karyotypes of *P. roborovskii* (a) and *P. sungorus* (b). Note that the Y chromosome and one arm of the X chromosome are completely heterochromatic in both species. All chromosomes were preidentified by Q-banding

(Fig. 1b). The NORs of *P. sungorus* are localized on the short arm telomeres of chromosomes 5, 7, 12 and 13 (Fig. 3b). Secondary constrictions were not observed in this species (Fig. 1a). This is in agreement with the results of Bigger and Savage (1976). With the exception of the NORs in chromosome 12 of both hamster species, there is no homoeology between the chromosomal sites of nucleolus organizer regions. One can hypothesize, that the common ancestor of *P. roborovskii* and *P. sungorus* had NORs not only in terminal positions, but also in interstitial positions. In the karyotypic evolution of *Phodopus*, the interstitial NORs could have been shifted to terminal positions by small pericentric inversions. On the other hand, terminal NORs could have been lost due to

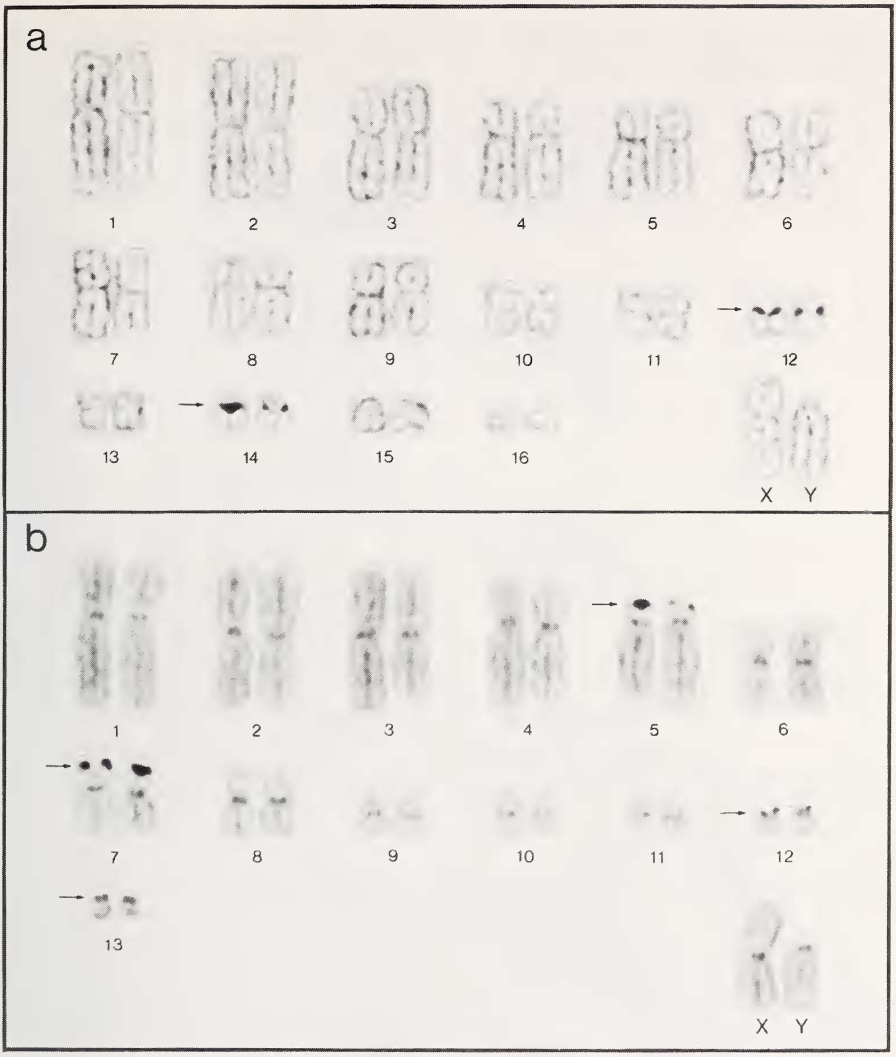

Fig. 3. Silver (Ag)-stained karyotypes of *P. roborovskii* (a) and *P. sungorus* (b). The arrows indicate the silver precipitation at the nucleolus organizer regions (NORs). All chromosomes were preidentified by their Q-bands

deficiences of NOR-associated heterochromatin or translocated onto other telomeric regions.

Figure 4 compares the R-banding patterns of *P. sungorus* (S) with those of *P. roborovskii* (R). The presumed chromosome homoeologies are demonstrated in the table. Because *P. sungorus* has lower number of chromosomes than *P. roborovskii,* the chromosome complement of this species is used as a basis for the alignment of homoeologous chromosome arms and segments. Six chromosomes of *P. sungorus* and *P. roborovskii* show a completely identical banding pattern: S3 = R2, S7 = R8, S8 = R9, S9 = R10, S13 = R16 and SY = RY. Four chromosomes differ only in their amount of constitutive heterochromatin: S10 = R11, S11 = R13, S12 = R12 and SX = RX. There is always more

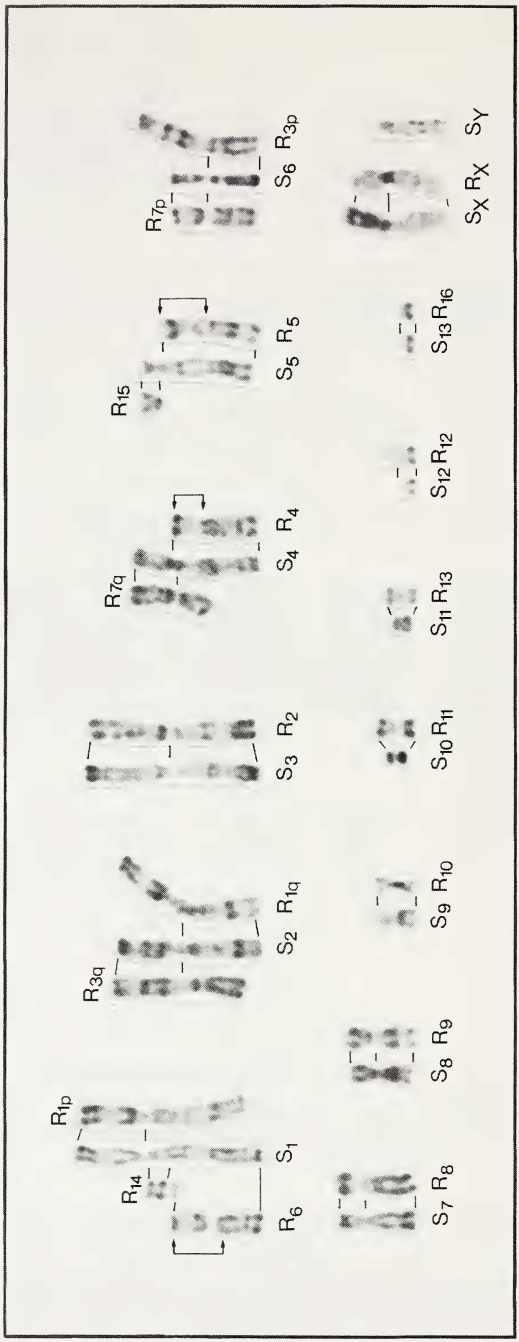

Fig. 4. A comparison of R-banding patterns between *P. roborovskii* (R) and *P. sungorus* (S). The chromosomes are arranged to align homoeologous chromosome segments. All chromosome arms or segments situated between two black dashes are homoeologous. The double arrows in chromosomes R4, R5 and R6 indicate the sites between which an inversion occurred

pericentromeric heterochromatin localized in the autosomes of *P. roborovskii*, whereas the heterochromatin in the short arm of SX is distinctly larger than in RX (Fig. 2). The biarmed chromosomes S2, S4, S5, S6 and R1, R3, R7 arose by a series of seven independent centric fusions, which occurred in acrocentric chromosomes of the ancestral karyotype.

The biarmed chromosomes R4, R5, R6 developed by pericentric inversions in acrocentric chromosomes. A comparison of the R-banding patterns of *Phodopus* indicates a very complex derivation for the chromosome S1. Two originally acrocentric chromosomes (corresponding to R6 and R14) initially formed a single biarmed chromosome. A subsequent telomeric fusion involving the short arm of this chromosome (R14) and the short arm of a further acrocentric chromosome (corresponding to R1p) then gave rise to S1. Interestingly enough, a large interstitial C-band is still identifiable in the long arm of chromosome S1 at exactly the site where the centric fusion should have occurred.

Table

Chromosomal homoeologies between *P. sungorus* and *P. roborovskii*

P. sungorus	*P. roborovskii*
1p	1p
1q	6inv + 14
2p	3q
2q	1q
3	2
4p	7q
4q	4inv
5p	15
5q	5inv
6p	7p
6q	3p
7	8
8	9
9	10
10	11
11	13
12	12
13	16
X	X
Y	Y

p = short arm; q = long arm; inv = pericentric inversion

The structure and behaviour of the sex chromosomes of *Phodopus* during male meiosis is demonstrated in figure 5. Using the C-banding technique, the X and Y chromosomes can be very distinctly localized in the various stages of meiotic prophase and diakinesis, due to their exceptionally large heterochromatin content (Fig. 2). The strongly stained sex vesicle, which consists of the condensed X and Y chromosomes, appears during late pachytene (Fig. 5a) and unfolds again at diplotene stage. In both hamster species, the sex vesicle consists of a dark (heterochromatic) and a light (euchromatic) region: the light region, which corresponds to the long arm of the X chromosome, consists of a rolled-up thread, which has the appearance of a tail in some of the later pachytene stages. During meiotic prophase and diakinesis, the pairing heterochromatic arms of the X and Y are highly condensed, whereas the non-pairing euchromatic arm of the X chromosome exhibits a dramatic delay of chromatin condensation. Usually, the unpaired arm of the X chromosome appears to be two to three times longer than the arm pairing with the Y chromosome. At diakinesis, the sex chromosomes have regained their normal morphology and exhibit a characteristic end-to-end association (Fig. 5b–e). The XY bivalent can be distinguished from the rod- to ring-like autosomal bivalents by its heteropycnotic appearance. C-banding enabled us to interpret the exact arrangement of the X and Y chromosomes in the bivalent configuration: the heterochromatic arm of the X chromosome is terminally associated with the distal part of the long arm of the Y chromosome. The end-to-end arrangement of the X and Y at diakinesis is interpreted to be the result of a partial synapsis followed by a single crossing over and subsequent terminalization (Solari 1974). The large autosomes usually exhibit two to three chiasmata, whereas the medium-sized ones have only one or two. An analysis of 300 meiotic cells in diakinesis and metaphase II showed a nondisjunction (ND) frequency of 2.2 % for the species *P. sungorus*. This value is approximately within the expected range (Long 1978).

Discussion

The karyotypic comparison between *P. sungorus* and *P. roborovskii* confirms that Robertsonian fusions and pericentric inversions are the most common mechanisms of structural

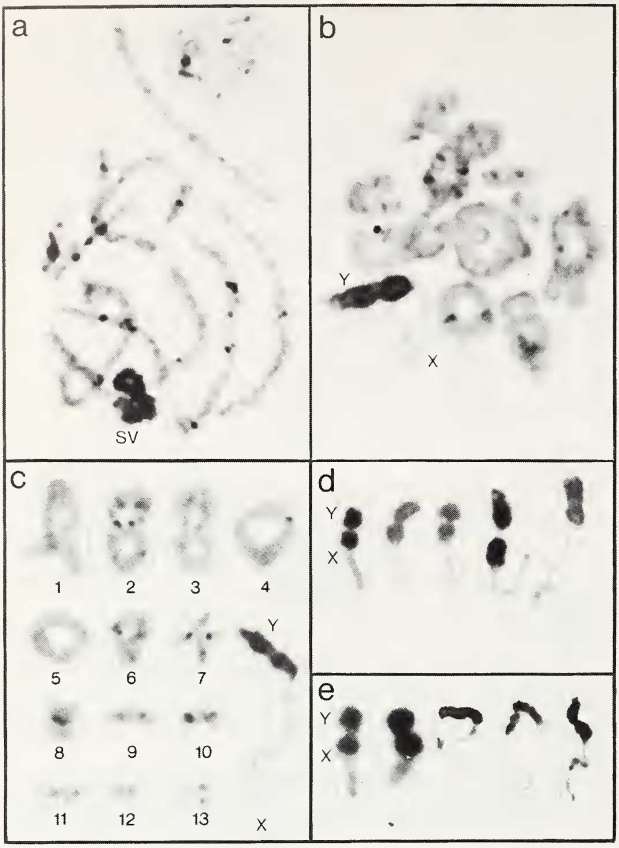

Fig. 5. C-banded meiotic chromosomes of *P. sungorus* (a–d) and *P. roborovskii* (e). (a) Late pachytene stage with prominent sex vesicle (SV). (b) Diakinesis. (c) Autosomal bivalents and XY bivalent of one diakinetic plate. (d, e) Cut-outs of sex bivalents from selected diakineses of *P. sungorus* (d) and *P. roborovskii* (e). The heterochromatic Y chromosome always associates end-to-end with the terminal segment of the heterochromatic arm of the X chromosome. Note the lower degree of chromatin condensation in the unpaired arm of the X chromosome

chromosome changes in the course of karyotypic evolution (Capanna et al. 1976; Fredga 1977; Viegas-Péquignot et al. 1983). The chromosome arms present in the karyotype of the common ancestor of *Phodopus* have been conserved as units in all chromosomes. The results of this study indicate that the karyotypes of *P. sungorus* and *P. roborovskii* evolved from an ancestral karyotype with a diploid complement of 2n = 40 comprising 7 metacentric or submetacentric chromosomes (including the X) and 14 acrocentrics (including the Y). After divergence of the two species, more of the ancestral chromosomes were conserved in the *P. roborovskii* line than in the *P. sungorus* line. The karyotype of *P. sungorus* is more complex than that of *P. roborovskii*. In the course of evolution, Robertsonian fusions seem to have caused a reduction of the chromosome number in both species. The different numbers of chromosomes in *P. roborovskii* (2n = 34) and *P. sungorus* (2n = 28) can be explained by the fact that some chromosome arms of *P. sungorus* correspond to discrete chromosomes in *P. roborovskii*. The long arm of chromosomes 1, 4 and 5 of *P. sungorus* is formed by the chromosomes 6 + 14, 4 and 5 of *P. roborovskii*. The long arm of chromosome S1 additionally contains a small chromosome of *P. roborovskii* (R14). The short arm of chromosome 5 of *P. sungorus* corresponds to chromosome 15 of *P. roborovskii*.

In addition to the structural chromosome rearrangements, marked differences were found in the amount of constitutive heterochromatin as well as in the localization of nucleolus organizer regions between *P. sungorus* and *P. roborovskii*. However, this fact does not interfere with the results obtained with R-banding patterns and the presumed

chromosome homoeologies. Changes in the position and quantity of constitutively heterochromatic regions are well documented among closely related species in various mammalian genera (Pathak et al. 1973; Patton and Sherwood 1982; Robinson et al. 1983). C-band heterochromatin is composed to a large extent of highly repetitive DNA sequences (satellite DNAs) which are not transcribed into RNA for protein synthesis. Because heterochromatin variations do not produce an obvious phenotypic effect, it is not surprising that these highly repetitive DNAs can evolve very rapidly (Yunis and Yasmineh 1971). The chromosomal distribution of nucleolus organizer regions is also known to differ significantly both within and among species (Schwarzacher and Wachtler 1983).

In several hamster species of the family Cricetidae, the sex chromosomes are of exceptional size. The X chromosome comprises about 10 % of the genome and the Y is always remarkably longer than the smallest autosomes. The X chromosome of *P. sungorus* makes up 9.9 % of the haploid female karyotype, the X chromosome of *P. roborovskii* makes up 6.7 %. For comparison, the X chromosome of *Mesocricetus auratus* constitutes 10.2 % and that of *M. newtoni* 7.4 % of the haploid genome (Voiculescu 1974). In general, the mammalian X chromosome comprises only approximately 5 % of the haploid genome and the Y chromosome is one of the smallest chromosomes of the complement (Ohno 1967). In the evolution of Mammalia, the euchromatic part of the X chromosome has become highly conserved and many identical X-linked genes are mapped on the X chromosomes in various mammalian species. When the size of the mammalian X chromosome exceeds 5 % of the haploid complement, the additional chromatin is usually genetically inert constitutive heterochromatin (Pathak 1983). Therefore, the large X and Y chromosomes of the Cricetidae may be caused by the addition of C-band heterochromatin to the original types of sex chromosomes during karyotypic evolution (Pathak and Stock 1974). The additional heterochromatin of the X and Y chromosomes leads to a characteristic behaviour of the sex bivalent.

This study presented a detailed comparison of the mitotic and meiotic chromosomes of two closely related hamster species. Karyotypic analysis permitted the reconstruction of the various structural chromosome rearrangements that have occurred during speciation of *Phodopus*. The results demonstrate that chromosomal evolution in closely related species can proceed in a very conservative manner, keeping entire chromosome arms as units.

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Zusammenfassung

Vergleichende zytogenetische Untersuchungen an den Hamstern Phodopus sungorus und P. roborovskii (Rodentia, Cricetinae)

Die mitotischen und meiotischen Chromosomen der beiden Hamster-Spezies *Phodopus sungorus* und *P. roborovskii* wurden mit Hilfe verschiedener Bänderungsmethoden untersucht. *P. sungorus* weist eine diploide Chromosomenzahl 2n = 28 auf, *P. roborovskii* 2n = 34. Die vergleichende zytogenetische Untersuchung zeigt sehr deutlich, daß die Karyotypen-Evolution bei nahe verwandten Spezies in einer konservierenden Art und Weise abläuft, wobei die Chromosomenarme des ancestralen Karyotyps als komplette Einheiten erhalten bleiben. Für alle euchromatischen Segmente können fast vollständige Homoeologien nachgewiesen werden. Die Unterschiede in den Karyotypen von *P. sungorus* und *P. roborovskii* können auf acht unabhängige zentrische Fusionen, drei perizentrische Inversionen, eine fragliche Telomer-Fusion, sowie auf Veränderungen in Gehalt und Anordnung des konstitutiven Heterochromatins zurückgeführt werden. Die Karyotypen beider Spezies haben sich mit einer hohen Wahrscheinlichkeit von einem gemeinsamen Vorfahren mit 2n = 40 Chromosomen entwickelt. Dabei ist der ancestrale Zustand der Chromosomen bei *P. roborovskii* eher erhalten geblieben als bei *P. sungorus*.

Auffallend sind in beiden Spezies die großen, heteromorphen Geschlechtschromosomen. Der

kurze Arm des X-Chromosoms und nahezu das gesamte Y-Chromosom bestehen aus konstitutivem Heterochromatin. In der männlichen Meiose zeigt der nicht mit dem Y-Chromosom gepaarte euchromatische Arm des X-Chromosoms eine stark verzögerte Kondensierung während der gesamten Prophase.

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